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## A New Species of Giant, Montane *Phrynobatrachus* (Anura: Ranidae) from the Central Mountains of Kenya

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A new species of large forest-dwelling frog of the genus *Phrynobatrachus* Günther (Ranidae) is described, based on material collected in two different montane localities in central Kenya. The new species differs in at least 10 characters from *Phrynobatrachus krefftii* Boulenger, an endemic to the Eastern Arc Mountains of Tanzania, and the only other large species of the genus in East Africa. A comparison of selected internal morphological character states among *P. krefftii*, the new species and several other species of the genus *Phrynobatrachus* suggests that the new species and *P. krefftii* are not closely related.

The ranid genus *Phrynobatrachus* Günther, 1862 is a poorly understood group. Individuals collected in the field are often difficult to identify to species, and past workers have frequently confused members of this group with cryptic, leaf-litter species of other genera including *Arthroleptis*, *Schoutedenella*, *Phrynodon* and *Dimorphognathus*. The few external characters that distinguish *Phrynobatrachus* from other genera include presence of a tarsal tubercle, absence of mandibular odontoids (present in *Dimorphognathus* and *Phrynodon*) and absence of a median dorsal skin raphe (present in *Arthroleptis* and *Schoutedenella*).

Of the 65 species of *Phrynobatrachus* listed in Frost (1985), many are based on scanty descriptions. Because of their cryptic nature, few species exhibit obvious, easily recognizable field characteristics upon which descriptions or identifications can be based; an exception is *P. cricogaster* (Perret 1957). Many species also exhibit a high degree of polymorphism (Stewart 1974). To date, few advertisement calls of *Phrynobatrachus* species have been analyzed or published.

Herein, we describe a new species which is apparently endemic to the central mountain massif of Kenya. This description is based on material collected at two separate localities between 20 and 30 years ago and deposited in four different institutions where it has remained unnoticed until recently. Institutional abbreviations follow Leviton et al. (1985).

## SPECIES DESCRIPTION

*Phrynobatrachus irangi*, n. sp.

Plate 1 and Fig. 1

HOLOTYPE. — MHNG 2230.76 male; KENYA: Meru District: Irangi Forest, above Irangi Forest Station, springs of Ena Stream. 0°24'S, 37°28'E, elevation 2100 m. Collected by J.-L. Perret and V. Mahnert, 12 October 1977.

PARATYPES. — MHNG 2230.74–75 males, MHNG 2230.77 sub-adult, MHNG 2230.78 female; CAS 158967 male, CAS 158966 (male, cleared and stained); AMNH 68808, 68810–11, AMNH 72854–56 males; AMNH 68790, 68809, 72853 females: vicinity of type locality, collected by R. Keith, 4 March, 28 April, 8 May, 1962 at 1965 m and 2286 m.

DIAGNOSIS. — A new montane species of *Phrynobatrachus* from the Kenya Massif and the Aberdare Range differing from all East African congeners in the large size of the females (to 51.0 mm), and from the large Tanzanian Highlands species *P. krefftii* in the following external (1–6) and internal (7–11) characters: (1) reduced webbing of the foot, (2) smaller inner metatarsal tubercle, (3) longer fifth toe, (4) central plantar surface of foot in breeding males with spiny asperities, (5) snout in breeding males rounded, not sharply projecting; (6) breeding males without dark outlining of lower jaw and without chrome yellow gular coloration, (7) nasals widely separated, not greatly dilated medially, not overlapped posteriorly by sphenethmoids, (8) neural spines of vertebrae not strongly imbricate, (9) base of omosternum not bifurcate, (10) base of thyrohyal originating well posterior to base of posterolateral process of hyoid, and (11) sternal style semi-rectangular, not strongly tapered medially.

ETYMOLOGY. — The specific epithet, a noun in apposition, refers to the type locality, Irangi Forest, Meru District, Kenya.

DESCRIPTION OF HOLOTYPE. — Male, 46.0 mm snout-vent length; habitus stout, robust; snout protruding but rounded, not sharply angled (Fig. 2); diameter of eye 4.5 mm, slightly more than half the distance to tip of snout, nearly equal to interorbital space; tympanum an oblique oval, its diameter approximately three-fourths that of eye and situated beneath a dermal fold that originates from mid-point of posterior margin of eye, curves ventrally around tympanum and terminates midway between angle of jaw and origin of forelimb; tip of fingers and toes rounded, only slightly dilated; tip of each toe in males with one or two lateral spines; webbing between fingers absent, webbing between toes reduced (Fig. 3) webbing formula I2-2+III1-2+III3-3IV3+-2+V (Savage and Heyer 1997); subarticular tubercles of both hands and feet single, palmar surfaces smooth, plantar surfaces beset with numerous, small, pale-colored spinose asperities, especially conspicuous along axes of fourth and fifth metatarsals (Fig. 3); large, thick greyish, granular nuptial pad extending from origin of thumb to just beyond proximal subarticular tubercle; tarsal tubercle a pale-colored eminence capped by white spine; fore- and hindlimbs stout, muscular; hindlimb length 2.5 times greater than snout-vent length; inner metatarsal tubercle white, small, about one-third diameter of eye.

Dorsum generally smooth in appearance but beset with widely spaced, very small, white-pointed tubercles that extend laterally to mid-lateral surface of body; thin, glandular ridge extends from the posterior margin of each eye, angling medially to level above posterior extent of tympanum but not converging with its fellow; a second, more posterior pair of slightly shorter, thin glandular ridges diverges obliquely in reverse direction to position above mid-point of forelimb insertion, forming following configuration:

$$\begin{array}{c} \backslash / \\ / \backslash \end{array}$$

dorsal skin of forelimbs smooth, hindlimbs smooth in femoral region but becoming increasingly tuberculate from midpoint of tibio-fibula to foot; posterior surface of thighs generally smooth with

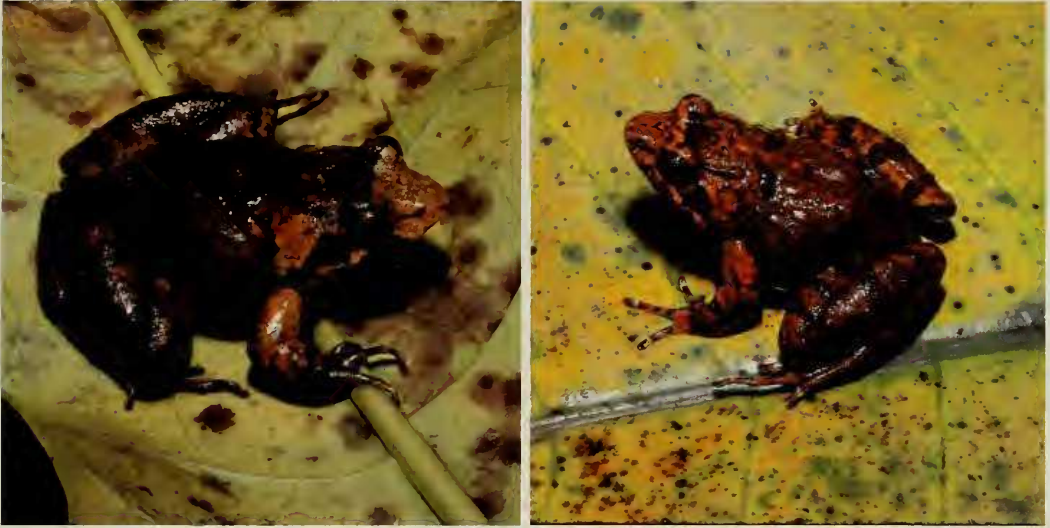


PLATE 1. A. (left) Holotype of *Phrynobatrachus irangi* (MHNG 2230.76). B. (right) Paratype (MHNG 2230.75). Photos by JLP in type locality, Irangi Forest, Kenya.

white-tipped, small spinous tubercles interspersed with larger flattened warts; ventral surface of body smooth, except for gular region, which consists of series of longitudinal, unpigmented, distensible folds comprising the vocal pouch.

Color in preservative. Ground color a medium, muddy brown; pale areas darkish beige; ventrum pale beige. Entire snout pale-colored, separated from darker dorsal coloration by sharply demarcated line across interorbital space including anterior one-third of each eyelid; pale area extending ventro-laterally and obliquely onto upper lip from anterior margin of eye; upper lip dark from posterior margin of pale patch and below eye to anterior margin of tympanum; tympanum dark; rounded pale patches extend antero-dorsally from anterior margin of origin of forelimbs to lateral margins of anterior pair of glandular ridges, and distally onto anterior surfaces of forearms to point near wrists; dorsal aspects of hands dark with darker band near each wrist; hindlimbs with nine, roughly equally-spaced, dark bands extending from thighs to feet; ventrum immaculate.

Color in life (Plate 1A). Dorsum dark brown; entire snout light orange-brown, sharply demarcated by transverse line running between eyelids; large patch of same contrasting color on shoulder, upper arm and elbow; hind limbs pale brown with dark, thick transverse bands; ventrum yellowish tan; gular region somewhat grayish.

VARIATION IN PARATYPES. — Morphological features in the paratype series are generally consistent with those described in the holotype. All female and a few male (AMNH 72854–72856) specimens lack small, pale dorsal and lateral spines; these are present in all remaining male specimens. Some variation exists in the plantar spines: plantar spines in the fourth metatarsal area are absent in the largest females (AMNH 72853 and AMNH 68790), present but reduced in females AMNH 68809 and MHNG 2230.78; present but reduced in males AMNH 72854, 72855 and 72856. Males AMNH 72854–72856 are soft and rather poorly preserved in comparison with the rest of the type series including males AMNH 68808, AMNH 68810–68811; these specimens are adults (snout-vent length 36.6–45.7 mm) so absence of dorsal and lateral spines in males is probably an artifact of preservation. Tarsal tubercles also vary; some individuals have a row of small tarsal spines, the largest and most posterior of which also occupies the position typical of tarsal tubercles in other species in the genus.

All specimens in the type series are consistent in dorsal color pattern with minor variations in intensity of ground color; all specimens exhibit the sharply-defined, pale-colored snout except one male



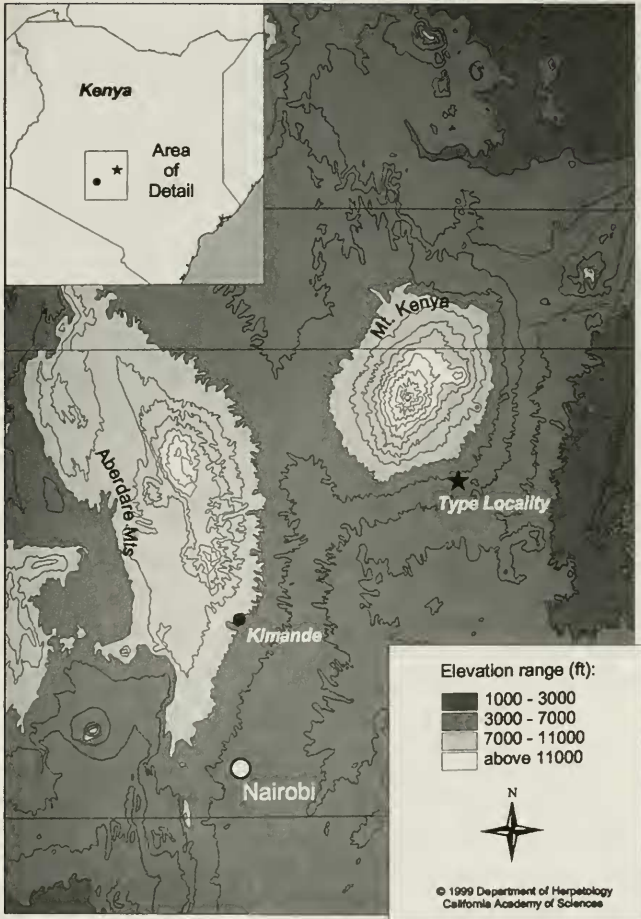


FIGURE 1. Type locality of *Phrynobatrachus irangi* sp. nov.: Irangi Forest, Mount Kenya, and location of Aberdare Range population (NMK specimens): former farm of Edna Oxtoby at Kimande, Kenya.

**VOICE.** — The advertisement call of *Phrynobatrachus irangi* has been recorded (Perret) from a chorus of many males; evidently no single voice was close enough for sonographic analysis. The call is rather loud and evidently emitted during the day only. It was described by R. Keith (in her field notes, AMNH Archives) as “rough-araugh-aaaaraugh-arararaugh-raraugh.”

## COMPARISONS

### External Morphology

The only other species of large *Phrynobatrachus* in East Africa, *P. krefftii* Boulenger, 1909, is endemic to the Eastern Arc Mountain system (Howell 1993). In Table 1, we have summarized meristic data taken from the type series of *P. irangi* and 16 males and females of *P. krefftii* from Amani, East Usambara Mountains, Tanzania (see Additional Material Examined). Whereas adult males of both species are comparable in size, adult *P. irangi* females attain much larger snout-vent lengths; in fact, female *P. irangi* may be the largest member of the genus *Phrynobatrachus*.

paratype (MHNG 2230.75) in which the snout is darker brown, but still demarcated by a pale orange-brown transverse bar (Plate 1B). One male specimen (AMNH 68808) has a thin, mid-dorsal pale stripe extending from the posterior margin of the pale snout patch to the tip of the urostyle; one female (MHNG 2230.74) is darker and more mottled in dorsal aspect than the remaining specimens. Supratympanic, rounded pale patches are discernable in six males (CAS 158967, MHNG 2230.74, AMNH 68808, 72854, 72855); these are less obvious in females and the remaining male specimens.

Ventral surfaces of three males (MHNG 2230.78, AMNH 68780, AMNH 68809) have diffuse greyish mottling that extends posteriorly from the gular region to the underside of the thighs; the underside in AMNH 72853 is immaculate; the venters of three males (AMNH 68811, 72855 and MHNG 2230.77) are also mottled but less so than in females; the ventral surface of the hindlimbs in male AMNH 72854 is moderately mottled in pale brown.

Measurements of the type series, and meristic comparisons with *Phrynobatrachus krefftii* are summarized in Tables 1 and 2.

Both male and female *P. irangi* have longer hindlimbs than *P. krefftii*, but smaller inner metatarsal tubercles. The tarsal tubercle of *P. irangi* is larger and more conspicuous than that of *P. krefftii*, which tends to be a single, small, spinous eminence at the terminus of a curved skin fold that originates near the posterior margin of the inner metatarsal tubercle. However, in some specimens of both species a series of small tubercles are present, with the largest occupying the posterior-most position. The plantar surfaces of the fourth metatarsal are spinose in male *P. irangi*, and smooth in *P. krefftii*. The presence of these small asperities on the ventral surfaces of the toes and feet, while differently distributed in these two species, appears to be a unique character within the genus *Phrynobatrachus*. Specimens of *P. krefftii* have more extensive webbing between the toes than do *P. irangi* (Fig. 3; webbing formula for *P. krefftii*: II-III0-0III1-2IV2+1V [Savage and Heyer 1997]).

Breeding male *P. krefftii* have a pointed, projecting, shallow snout in lateral profile (Fig. 2); the lower jaw is sharply defined by dark pigment which, in turn, is outlined medially by starkly contrasting white pigment. The gular region is bright chrome yellow in life (Barbour and Loveridge 1928). In preservative, the yellow gular region of male *P. krefftii* fades to the same color as the venter, but the strongly marked coloration of the lower jaw persists. Male *P. irangi* have rounded, less-projecting snouts, the lower jaw is mottled, not evenly outlined, and the bright chrome yellow gular coloration of *P. krefftii* males is absent.



FIGURE 2. Right lateral aspects of *Phrynobatrachus irangi* male holotype (MHNG 2230.76) (above); *Phrynobatrachus krefftii* male CAS (186541) (below).

TABLE 1. Measurements of type series of *Phrynobatrachus irangi*. Mean (in mm) followed by range (in parentheses).

	n	SVL	Tibia	T/SVL (%)	Foot	F/SVL (%)	T/F (%)
<i>P. irangi</i> (male)	14	41.7 (36–46)	25.8 (21–27)	58.7 (54.7–62.3)	26.2 (21–29)	63.2 (53.4–64.0)	105.7 (93.1–108.6)
<i>P. irangi</i> (female)	4	45.7 (45–51)	24 (22–26)	53.1 (48.9–58.25)	25.7 (24–28)	55.6 (47.05–63.4)	95.1 (88.5–108.3)

TABLE 2. Comparison of mean measurements (in mm) of *Phrynobatrachus irangi* and *P. krefftii*.

	SVL	Tibia	T/SVL (%)	Foot	F/SVL (%)	T/F (%)	MT
<i>P. irangi</i> (male)	41.7	25.8	56.7	26.2	63.2	105.7	1.7
<i>P. krefftii</i> (male)	41.0	21.8	53.4	24.2	59.4	89.9	2.4
<i>P. irangi</i> (female)	45.7	24.0	53.1	25.7	55.6	95.1	1.6
<i>P. krefftii</i> (female)	38.4	18.2	47.6	19.6	51.0	93.3	2.05



FIGURE 3. (left) Right foot in plantar view of male *P. krefftii* (NMK A/883.11); (right) *P. irangi* male paratype (MHNG 2230.75).

### Internal Morphology

Examination of cleared and double-stained specimens reveals notable differences between the two species. In dorsal view, the nasals of *P. irangi* are widely spaced, not greatly dilated medially and are not overlapped posteriorly by the sphenethmoids; *P. krefftii* nasals are more broadly dilated medially, less widely spaced, and overlapped by anterior projection of the sphenethmoids (Plate 2A, B).

The presacral vertebrae in *P. krefftii* are strongly imbricate; those of *P. irangi* are non-overlapping (Plate 2A, B).

Viewed ventrally, the base of the omosternum in *P. irangi* is slightly notched; that of *P. krefftii* is moderately forked (see states 16.1 and 16.2, in Drewes 1984). The sternal style of *P. irangi* is near-rectangular, only slightly compressed medially, with a medial width greater than half the width of the anterior margin; that of *P. krefftii* is compressed medially, so that the medial width is half the width of the proximal margin of the structure. (Plate 2C, D)

In *P. irangi*, the bases of the thyrohyals originate posterior to a line drawn through the bases of the posterolateral processes; in *P. krefftii*, the thyrohyals are deeply invasive into the corpus of the hyoid plate and extend anterior to the bases of the posterolateral processes (Plate 2C, D)

In an attempt to ascertain the degree of relatedness between *P. irangi* and *P. krefftii*, the internal characters that serve to separate the two were examined in cleared and stained specimens of eight additional species of *Phrynobatrachus* (see Additional Specimens Examined). A phenogram, a UPGMA tree generated by PAUP 4.0b1 (Fig. 4) was based on the character matrix in Table 3. An additional state of character 1, degree of separation of nasals, was found in the added species, and coded "M". The phenogram, indicates that in spite of large size and gross similarity between *P. irangi* and *P. krefftii*, they probably are not closely related. *Phrynobatrachus irangi* shares more of its diagnostic character states with *P. parvulus* and *P. parkeri* than with the rest of the group; based on the same characters, *P. krefftii* clusters with *P. dendrobates*.

The states of four characters (neural arch, omosternum, sternal style and separation of nasals) were polarized using works by Clarke (1981), Drewes (1984), Lynch (1973) and a data set on petropedetine ranid genera (Drewes, unpublished). PAUP was employed in an attempt to assess the phylogenetic positions of *P. krefftii* and *P. irangi* with respect to each other and the relatively small sample of additional species in the genus (15%, see Frost 1985). The resulting analysis yielded 311 most parsimonious trees and was not resolvable; however, it indicated that with respect to a presumptive ancestor, *Phrynobatrachus irangi*, *P. kinangopensis*, *P. natalensis*, *P. parvulus*, *P. versicolor*, *P. parkeri*, *P. perpalmatus*, and *P. plicatus* form an unresolved polytomy, but are more closely related to each other than any is to *P. krefftii* and *P. dendrobates*. The latter form a basal clade with respect to the former. Interestingly, calling males of *P. dendrobates* share the characteristic bright, chrome yellow gular region of *P. krefftii* males.

Both *P. irangi* and *P. krefftii* share spinous asperities in the subdigital areas of the feet, as well as on the terminal discs, although the distribution of these asperities on plantar surfaces is consistently different between the two species. To our knowledge, possession of this character state is unique to these two species within the genus *Phrynobatrachus*; we posit that the appearance of this character



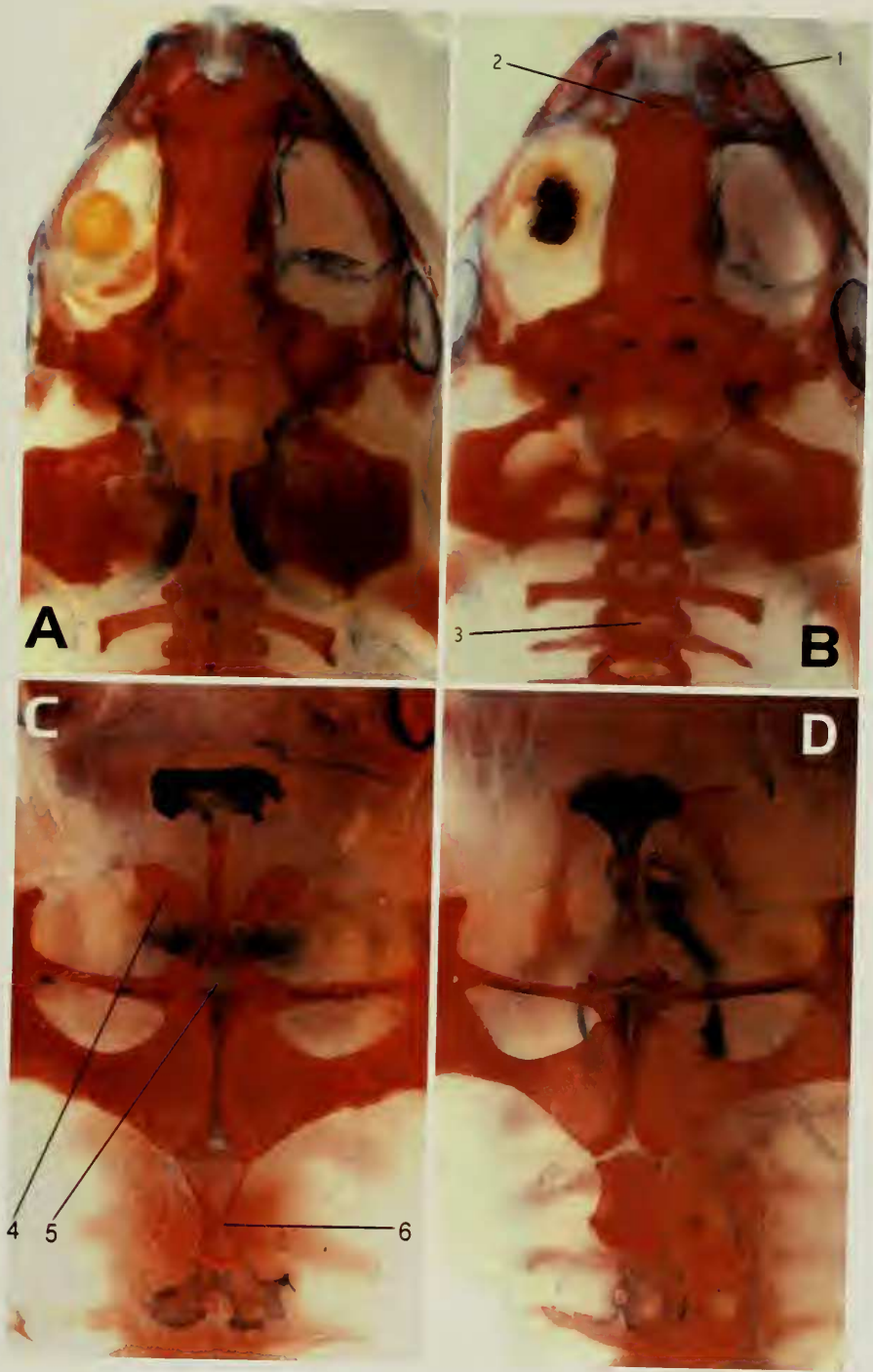


PLATE 2. Dorsal and ventral views of cleared and double-stained specimens of *Phrynobatrachus krefftii* (A, C, BM 1974.80) and male paratype *Phrynobatrachus irangi* (B, D, CAS 158966). Key: 1. nasal, 2. sphenethmoid, 3. non-imbricate neural arch, 4. base of thyrohyal, 5. base of omosternum, 6. sternal style.

TABLE 3. Distribution of internal character states differentiating *P. irangi* from *P. krefftii* among other *Phrynobatrachus* species.

	1	2	3	4	5	6	7
<i>P. dendrobates</i>	M	K	K	K	K	K	K
<i>P. kinangopensis</i>	I	I	I	I	K	I	K
<i>P. natalensis</i> (2)	M	K	I	I	I	I	I
<i>P. parvulus</i>	I	I	I	I	I	I	I
<i>P. versicolor</i>	I	K	I	I	K	K	I
<i>P. parkeri</i>	I	I	I	I	I	K	I
<i>P. perpalmatus</i>	I	K	K	I	K	I	I
<i>P. plicatus</i> (2)	M	K	K	I	K	K	I
<i>P. irangi</i>	I	I	I	I	I	I	I
<i>P. krefftii</i>	K	K	K	K	K	K	K

- Character states: 1. nasal separation at midline  
2. medial nasal dilation  
3. posterior nasal overlap by sphenethmoid  
4. neural arch imbrication (at least presacral vertebrae #1–3)  
5. omosternum bifurcation  
6. sternal style shape  
7. thyrohyal condition

K = state found in *P. krefftii*  
I = state found in *P. irangi*  
M = state found in some additional species, i.e., nasals narrowly separated or meet at midline

may be the result of convergence, possibly related to their large size or derived from living in montane habitats.

Natural history

Based on the field experience of Perret and R. Keith’s field notes, *Phrynobatrachus irangi* is active by day. Males were found calling on banks of small streams in the forest, from under roots or logs, and from holes in the mud. They were difficult to locate and capture. No amplexus has been observed, and although tadpoles were seen in nearby clear water, their identity was not ascertained.

DISCUSSION

The history of the material upon which this description is based is interesting and also necessary to document because of an error in the field data associated with the material from the National Museums of Kenya ([NMK], Additional Materials Examined). The specimens originally collected by E. Oxtoby at Kimande were first brought to the attention of Drewes in the early 1970s by the then Head of Herpetology at NMK. At that time, no attempt had been made on the part of NMK staff to collect further material, in spite of urging on the part of Oxtoby. Following Oxtoby’s death, Drewes and an NMK staff member, Peter Nyamenya, made a day trip to the former Oxtoby property in October 1979 and found it severely modified by local subsistence farming. No *Phrynobatrachus* were seen or collected. For the next several years, attempts on the part of Drewes to borrow the Oxtoby material from the National Museums of Kenya for purposes of description were fruitless, and it was assumed that the Oxtoby material had been misplaced or lost.



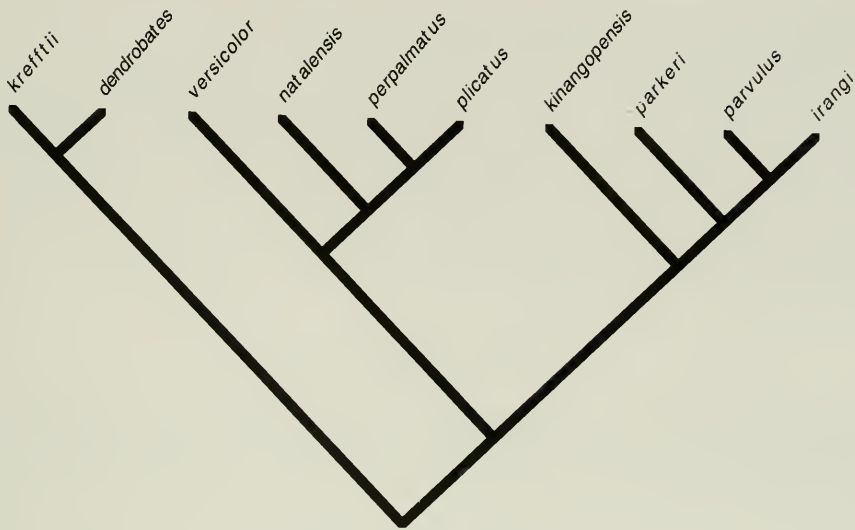


FIGURE 4. UPGMA Phenogram generated by PAUP, based on character states in Table 3.

During a visit to the MHNG in Geneva in 1985, Perret showed Drewes a series of large *Phrynobatrachus* that he and V. Mahnert had collected in the Irangi Forest in 1979. Irangi is on the eastern slope of Mt. Kenya, while Kimande, the former Oxtoby property is on the south-southeastern slope of the Aberdares, a range of mountains some 90 km., as the crow flies (see Fig. 1), from the Irangi site. It became obvious to Drewes that if the two samples did not represent the same undescribed species, they were almost certainly, closely related species. It seemed unwise to describe the MHNG material without including the NMK material; attempts by both authors to borrow the NMK material continued to be unsuccessful. In 1993, Drewes queried Dr. Linda Ford of the American Museum of Natural History as to whether or not Ronald Keith, a field worker who made extensive collections in East Africa in the early sixties, had ever collected in the Irangi Forest. The response was positive and more than half of the type series described below is in the American Museum of Natural History.

In 1993, during a visit to the NMK, Drewes learned that the original Oxtoby Aberdares material had been found in a locked cabinet, and it has been included under Additional Material Examined. With respect to the NMK material, it is clear that the cataloged collection date of "1979" is in error; the specimens had to have been collected earlier, most likely in the early 1970s, inasmuch as the date of the day trip undertaken by Drewes and Nyamenya in 1979 is documented in photographs of the property taken at the time. The NMK specimens were not included as paratypes because the locality from which they were taken has evidently been destroyed, the population may be extinct, and we know of no field worker who has seen members of this population in life.

#### ADDITIONAL MATERIAL EXAMINED

*Phrynobatrachus irangi*: NMK A/1203/1-2, A/1203/4. Kenya: Murang'a Dist: Kimande. 0°49'S, 36°48'E; males, collected by E. Oxtoby, 30 April 1979(?); Kenya: Meru Dist: type locality: AMNH 68791-68793, AMNH 68795-68796, AMNH 135816. juveniles, collected by R. Keith, 1962.

*Phrynobatrachus krefftii*: CAS 168511-168557. Tanzania: Tanga Region: Muheza Dist: East Usambara Mtns, vic. of Amani.; BMNH 1974.79-91. Tanzania: West Usambara Mtns. Mazumbai

Forest Reserve, 4°48'S, 39°29'E; NMK A/883/7, A/883.11 males; A/883/16-17, females. Tanzania: East Usambara: Amani collected by B. Watulege, July 1969.

Cleared and Stained: *Phrynobatrachus dendrobates*, CAS 145294: Zaire: Ituri Prov: Manguerete Hipa; *P. kinangopensis*, CAS 152381: Kenya: Murang'a Dist: Kimande; *P. krefftii*, BM 1974.80: Tanzania: West Usambara Mtns: Mazumbai Forest Reserve; *P. natalensis*, CAS 141564: Kenya: Kakamega Dist: Kakamega Forest Station; CAS 141666: Kenya: Kakamega Dist: Lubao; *P. parvulus*, CAS 145258: Zaire: Kivu Prov: Fizi Terr: Mokanga; *P. versicolor*, CAS-SU 13008: Zaire: Kivu Prov: Albert N.P.: Kundhuru-ya-Tshuwe; *P. parkeri*, CAS 98168: Zaire: Uele: Monga; *P. perpalmatus*, CAS 98156: Zaire: Uele: Albert N. P.: Buta; *P. plicatus*, CAS 136294, 136298: Ghana: Eastern Reg.: Kade Agricultural Station.

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#### LITERATURE CITED

- BARBOUR, T. AND A. LOVERIDGE. 1928. A comparative study of the herpetological faunae of the Uluguru and Usambara Mountains, Tanganyika Territory with descriptions of new species. Mem. Mus. Comp. Zool., Harvard Univ. 50:86-265, 4 pls.
- CLARKE, B. T. 1981. Comparative osteology and evolutionary relationships in the African Raninae (Anura Ranidae). Monit. zool. ital. (N. S.) Suppl. 15:285-331.
- DREWES, R. C. 1984. A phylogenetic analysis of the Hyperoliidae (Anura): Treefrogs of Africa, Madagascar and the Seychelles Islands. Occ. Pap. Calif. Acad. Sci. 139:1-70.
- FROST, D. R., ed. 1985. Amphibian species of the world: a taxonomic and geographical reference. Assoc. Syst. Collections and Allen Press, Lawrence, Kansas. v + 732 p.
- HOWELL, K. M. 1993. Herpetofauna of the eastern African forests. Pp. 173-201 in Biogeography and ecology of the rain forests of Eastern Africa. J. C. Lovett and S. K. Wasser, eds. Cambridge University Press, United Kingdom.
- LEVITON, A. E., R. H. GIBBS, JR., E. HEAL, AND C. E. DAWSON. 1985. Standards in herpetology and ichthyology: Part 1, Standard symbolic codes for institutional resource collections in Herpetology and Ichthyology. Copeia 1985:802-832.
- LYNCH, J. D. 1973. 3. The transition from archaic to advanced frogs. Pp. 133-182 in Evolutionary biology of the anurans. J. L. Vial, ed. University of Missouri Press, Columbia, Missouri.
- PERRET, J.-L. 1957. Un nouveau *Phrynobatrachus* du Cameroun. Rev. suisse Zool. 46:527-531.
- SAVAGE, J. M. AND W. R. HEYER. 1997. Digital webbing formulae for anurans: a refinement. Herpetol. Rev. 28:131.
- STEWART, M. M. 1974. Parallel pattern polymorphism in the genus *Phrynobatrachus* (Amphibia, Ranidae). Copeia 1974:823-832.